FREQUENCY RATIOS OF SOAEs MATCH THE INTER-CELL SPACING OF OUTER HAIR CELLS: SUPPORT FOR A *SAW* MODEL OF THE COCHLEA

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A new resonance theory of hearing models the cochlea as a surface acoustic wave (SAW) resonator (1). This SAW model calls for outer hair cells (OHCs) to respond piezoelectrically to intracochlear fluid pressure, and, via associated electomotility, to generate slowly propagating surface tension waves (ripples) on the undersurface of the overlying tectorial membrane. Because OHCs are combined sensors and effectors, the ripples continue to reverberate between the precisely aligned rows of OHCs in the same way as electromechanical ripples do between the interdigital electrodes of a SAW resonator. The distance OHC1–OHC3 is 1 wavelength (360° phase delay). This mechanism is conjectured as providing the positive feedback and gain underlying the cochlear amplifier.

With isotropic ripple velocity, the frequency of the reverberating ripples is the inverse of the distance between OHCs. The cells lie in a periodic quasi-crystalline array that can be specified by 3 parameters: (i) the distance between rows ($b/2 \equiv 0.5$); (ii) the distance, a, between neighbouring cells in the longitudinal direction; and (iii) the tilt of the unit cell (face-centered rhomboid) away from the radial direction. Examination of published micrographs (1) reveals that, ignoring (iii) because it is small, the most commonly observed alignment in a range of animal species gives a/b of about 0.38, corresponding to a first oblique angle θ_1 of arctan 0.38 = 21°.

Ref (1) puts forward the idea that reverberation occurs not only between rows (in the radial or b direction), but also at oblique angles wherever an alignment of OHCs occurs, giving a series of reverberating cavities called L_0, L_1, L_2, L_3, L_4, L_5, L_7… This reverberation is taken to be the process underlying the generation of spontaneous emissions. The most common ratio between neighbouring SOAE frequencies in humans is observed to be 1.06 ±0.02 (a semitone), and that figure corresponds nicely to the ratio L_0:L_1 = 1/cos20° = 1.064. It is hypothesised that the OHCs detect ratios in tonal complexes by sensing simultaneous activity in reverberant cavities active in each arm of their stereocilia, a concept that opens up a fresh perspective on how our musical perception arises.

Closer examination of OHC lattices reveals that the tilt of the unit cell (factor (iii)) is about 4°. Cavity lengths predicted from this geometry (**Fig. 1**) match observed gaps in frequency ratios of SOAEs (**Fig. 2**). Significantly for music, the geometry of Fig. 1 generates many small-integer ratios such as 2:1 (L_{-1}:L_{-5}, L_1:L_5); 3:2 (L_{-1}:L_3); and 4:3 (L_3:L_{-5}, L_1:L_{-3}, L_{-5}:L_{-7})...

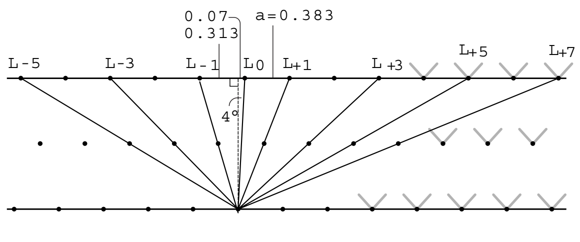

FIG. 1. Geometry of the OHC lattice (idealised from micrographs) generates a sequence of intercell distances in which there is an alignment of 3 OHCs. Simple trigonometry gives the lengths 1.048 (L_{-1}), 1.098 (L_{+1}), 1.471 (L_{-3}), 1.577 (L_{+3}), 2.099 (L_{-5}), 2.223 (L_{+5}), etc. In terms of inverse frequency, these form the sequence 1.000, 1.048, 1.404, **1.505, 2.003**, 2.121, 2.668, 2.793…

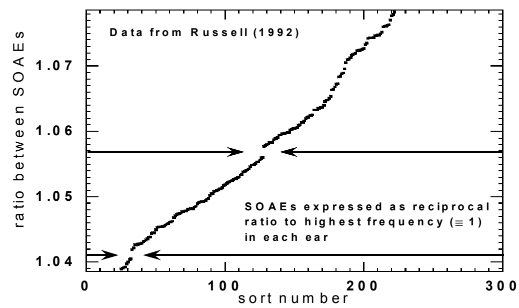

FIG. 2. Distinct gaps (arrows) occur in SOAE data at ratios of 1.057 and 1.041. Note from Fig. 1 that L_{-5}/L_5 = 1.059 and L_{-9}/L_9 = 1.038, suggesting that an SOAE in one arm of a resonant cavity precludes SOAE generation in the complementary arm.

1. Bell A. 'The Underwater Piano' <http://cogprints.soton.ac.uk/abs/bio/200005001>

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